

Consequences of an uncertain mass mortality regime triggered by climate variability on giant clam population management in the Pacific Ocean

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HIGHLIGHTS

- Quotas were the best management strategy regardless of the mortality regime.
- Climate variability decreased the efficiency of all management scenarios.
- Temporal autocorrelation in natural mortality increased the variability of stocks.

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ABSTRACT

Despite actions to manage sustainably tropical Pacific Ocean reef fisheries, managers have faced failures and frustrations because of unpredicted mass mortality events triggered by climate variability. The consequences of these events on the long-term population dynamics of living resources need to be better understood for better management decisions. Here, we use a giant clam (*Tridacna maxima*) spatially explicit population model to compare the efficiency of several management strategies under various scenarios of natural mortality, including mass mortality due to climatic anomalies. The model was parameterized by *in situ* estimations of growth and mortality and fishing effort, and was validated by historical and new *in situ* surveys of giant clam stocks in two French Polynesia lagoons. Projections on the long run (100 years) suggested that the best management strategy was a decrease of fishing pressure through quota implementation, regardless of the mortality regime considered. In contrast, increasing the minimum legal size of catch and closing areas to fishing were less efficient. When high mortality occurred due to climate variability, the efficiency of all management scenarios decreased markedly. Simulating El Niño Southern Oscillation event by adding temporal autocorrelation in natural mortality rates increased the natural variability of stocks, and also decreased the efficiency of management. These results highlight the difficulties that managers in small Pacific islands can expect in the future in the face of global warming, climate anomalies and new mass mortalities.

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1. Introduction

Small insular human communities will have to deal with many difficulties in the next decades to sustain their livelihoods in the face of climate change. In particular, fisheries are predicted to be severely jeopardized by climate variability (Bell et al., 2011). The future state of resources does not only depend on fishing pressure, but is also determined by this difficult-to-predict and

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difficult-to-manage climate variability. Changes are predicted to be unprecedented and projections remain challenging to make. The influence of climate on resources and livelihoods are major issues voiced by all island country leaders at recent international forums on climate change and policy (Bell et al., 2016; Schubert et al., 2017). Tools and models that can provide objective information to support decision-making in a changing climate era are needed.

Theoretical population dynamics and related tools have allowed assessing the sustainability of fisheries and building recommendations for their management. For instance, the management strategy evaluation (MSE) involves using simulation to compare the relative effectiveness of different management approaches for achieving specific management objectives. It has been widely used to assess the effectiveness of management strategies of fisheries, and identify poorly effective strategies that should be eliminated from further consideration (Butterworth et al., 2010; Punt et al., 2016). In practice, MSE involves an operational model (e.g., a population dynamic model) that provide a mathematical representation of the system to be managed, and the fishery that impacts the modelled population (Punt et al., 2016). This operational model can be a population model that allow linking the parameters that affect the life cycle at individual scale (e.g., growth, reproduction, mortality), and apprehend their effect at population level (e.g., stock, recruitment) (Caswell, 2001). The selection of the parameters of the operational model and assess their uncertainty is ideally performed by fitting the model to existing data (Punt et al., 2016). As a result, the recommended management strategies identified by the MSE are usually relevant for the past or present environmental and biological conditions. This means that the operational models implemented in MSE and parameterized with past or present conditions may not be relevant to assess what will happen to populations exposed to future environmental conditions. Unlike temperature latitude fisheries that monitored for stocks, capture sizes, recruitment levels, and other parameters for decades, there is a general paucity of data for tropical reef fisheries. Yet, solutions are urgently needed, as the small scale fisheries of island countries cannot afford waiting decades for data collection before analysing the possible efficiency of management scenarios.

An example of small-scale fishery in demand of management options is the giant clam fishery in the Central Pacific. Giant clams (family Cardiidae, subfamily Tridacninae) are exploited in the Central Pacific for their meat, shell, and for the aquarium trade (Neo et al., 2017; Van Wynsberge et al., 2016; Remoisenet and Wabnitz, 2012). To avoid stock depletion due to increasing commercial exports of meat and shells, all known Tridacninae species were listed in the Washington convention (CITES) in 1985. The trade and export of giant clams between signatory countries are therefore strictly regulated. Considering the wide distribution and relative abundance of one species, *Tridacna maxima*, compared with other giant clam species, *T. maxima* is classified as “lower risk/conservation dependent” (LR/CD) on the IUCN red list of endangered species (IUCN, 2012). The sustainability of giant clam resource appears therefore strongly dependent on historical fishing pressure, management measures, natural productivity, and resistance and resilience of populations to climate change (Black et al., 2011; Van Wynsberge et al., 2016; Neo et al., 2017).

In French Polynesia, the export of a limited number of wild giant clams for the aquarium trade is temporary authorized by CITES (SPC, 2013), provided that stocks are locally managed in a sustainable way. Stock assessments for nine island or atoll lagoons were conducted *in situ* in 2004/2005 (Tubuai and Raivavae islands from Austral Archipelago; and Reao, Pukarua, Napuka, Tatakoto, Fangatau, Tureia and Vahitahi atolls, eastern Tuamotu Gilbert et al., 2006). The spatial characterization of stocks led to the implementation of No Take Areas (NTA) in Tatakoto (Gilbert et al., 2005) and Reao, and supported the development of aquaculture in these two

atoll lagoons characterized by a high potential for successful spat collection (e.g., high densities and size structure oriented towards small individuals, Gilbert et al., 2006; Remoisenet and Wabnitz, 2012).

Despite the implementation of management measures and attempt to run sustainably giant clam fisheries, managers have faced a number of failures and frustrations because giant clam abundances have decreased drastically in several lagoons due to lethal environmental conditions at certain time (Adjeroud et al., 2001; Adessi, 2001; Barott et al., 2010; Andréfouët et al., 2013, 2015). Specifically at Tatakoto atoll, Andréfouët et al. (2013) reported a tenfold decrease of stocks between 2004 and 2012. For semi-closed atolls where connections between ocean and lagoon are only possible through few shallow channels usually located in the South part of the atoll rim, Andréfouët et al. (2015) could correlate the occurrence of mortality events with prolonged periods of high temperature, low swell and low wind from the South/South-East. These conditions dry up channels and prevent water renewal, and the lagoon becomes temporary closed and vulnerable to bio-physical disturbances (e.g., low water level, high temperature, variability in water salinity and nutrients). Mortality regimes may also be influenced by El Niño Southern Oscillation, with higher risk of giant clam bleaching during El Niño periods (Andréfouët et al., *in press*). Other hypotheses were considered to explain the decrease in stocks at Tatakoto (e.g., negative density dependence processes, predation, parasites, pathogen, see Van Wynsberge et al., 2017), but to date the relative importance of these ecological factors remain uncertain.

Beyond the temporal variability of stocks at the atoll scale, spatial differences in density were highlighted between lagoons and within lagoons (Gilbert et al., 2006). Differences in stocks at these scales could be related to differences in habitats, growth, natural mortality, and reproduction, which also varied between lagoons (Van Wynsberge et al., 2017). Indeed, higher mortality rates were reported in semi-closed atolls of Tuamotu archipelago compared with the open lagoon of Tubuai Island in Austral archipelago (Gilbert et al., 2007) and mortality rates varied spatially inside Tatakoto's lagoon (Van Wynsberge et al., 2017).

The high spatial and temporal variability of stocks and life traits complicate management as well as its efficiency over the long run. For example, the NTA at Tatakoto in 2004 was selected initially because of its high giant clam density and potential as a source population for the lagoon (Gilbert et al., 2005). A re-evaluation of stocks in 2012 revealed that this area was the most vulnerable to climatic anomalies (Andréfouët et al., 2013). This event, and other recent observations, have clearly changed the way benthic resource management should be designed in French Polynesian atolls. Specifically, instead of making management recommendations on the basis of presumably stable yields and resource, it seems sensible to take into account the climate-change related disturbances and stochastic processes that also dynamically shape the status of the resource.

Population models were used to make projections of giant clam stocks and compare the relative influence of various management scenarios (Yau et al., 2014; Van Wynsberge et al., 2013). However, no study thus far has compared the efficiency of management scenarios under various regimes of climate-induced mortality. To fill this gap, we integrate several datasets on growth, reproduction, natural mortality and fishing effort previously acquired for two lagoons of French Polynesia (Van Wynsberge et al., 2015, 2017) to build a spatially explicit population dynamics model. We then use the model to address three research questions: (i) Do theoretical models of population dynamics support the hypothesis that giant clam populations have been affected during the past decade by a mass mortality that occurred punctually and suddenly, as expected if triggered by climate variability? (ii) Which management strategies are the most efficient to manage population stocks considering

the current environmental conditions? (iii) Do these strategies remain efficient if climate variability increases, and mass mortality occurs, during the next century?

These questions are relevant to the giant clam context in French Polynesia, but can also contribute to theoretical population biology for many fisheries facing climate change. While the case is here specific to giant clam fishery, a demonstration on how to parameterize a model of population facing high risks of massive mortality, conduct sensitivity analysis, and discuss results would provide a theoretical and methodological baseline useful in many contexts.

2. Methods

This section describes first the two study sites and their relevance to address the research questions (Section 2.1). Then, the sampling methods used to monitor giant clam densities are described (Section 2.2), followed by the population model structure and its parameterization (Sections 2.3 and 2.4). In Section 2.5, we describe how field data have been used in our analysis to validate the model. Finally in Section 2.6, we describe the management strategies considered in the MSA and the method implemented to evaluate their effectiveness in various conditions of climate variability.

2.1. Study sites

Our study focused on two sites in French Polynesia: the semi-closed atoll of Tatakoto (138°24'W, 17°20'S) located in the Tuamotu Archipelago, 1200 km East of Tahiti; and the island of Tubuai (149°29'W, 23°22'S) located in the Austral Archipelago, 600 km South of Tahiti (Fig. 1a).

The two study sites are representative of two contrasting reef environments. The lagoon of Tubuai (90 km²) is open as it is permanently connected to oceanic waters through a large reef pass in the northern part of the lagoon and a small reef pass in the southwest end of the lagoon (Fig. 1b). The reef edges also consist of submerged reef flats and ridges, therefore exposing the lagoon to waves at high tide and during periods of strong swell. The atoll rim of Tatakoto is closed in its northern part, but the lagoon (11.46 km²) is connected to the ocean by several shallow channels that bisect the southern part of its rim (Fig. 1c). Tatakoto is therefore a semi-closed atoll (Andréfouët et al., 2001).

Together, these two sites provided a comparative framework, allowing to assess the robustness of our results to differences in lagoon environment. The two contrasted islands and environment also set a first baseline against which a wide number of islands in the Pacific Ocean can be compared with.

2.2. Monitoring of *T. maxima*'s densities

Assessment of stocks and size structure of *T. maxima* was achieved for a range of suitable habitats in April 2004 and January 2012 at Tatakoto, and in December 2004 and June 2010 at Tubuai (Gilbert et al., 2006; Andréfouët et al., 2013; Van Wynsberge et al., 2013) by combining remote sensing and field surveys. For this study, three and two supplementary surveys were performed at Tatakoto (November 2012, October 2013 and October 2014) and Tubuai (November 2013 and December 2014), but considered fewer stations than the initial surveys (Fig. 1). Only stations that were consistently surveyed during all the various field campaigns were considered here (See Appendix A1 in Supplementary Materials).

At Tubuai, 16 stations were repetitively surveyed during the decade. These stations covered the western and southern reef flats ($n = 3$ and $n = 2$), sedimentary terraces ridges ($n = 1$ and $n = 2$), the south-eastern lagoon patch reefs ($n = 3$), the western

lagoon patch reefs ($n = 1$), the north-eastern lagoon patch reefs ($n = 1$), the eastern reef flat ($n = 1$), the eastern fragmented reef flat ($n = 1$), and the south-eastern reticulated patch reef system ($n = 1$), all identified to hold distinct giant clam densities by previous studies (Gilbert et al., 2006).

The initial stock assessment performed at Tatakoto identified the Eastern and enclosed part of the lagoon as a unique entity due to the presence of mounds of very high clam densities (Gilbert et al., 2006). These mounds of high giant clam densities were not present in the wider western lagoon (Gilbert et al., 2006), which was subdivided according to depth. Indeed, the shallow (0.5–2 m) edges of lagoon pinnacles and inner reef flats held higher densities than deeper areas (>2 m) along the slopes of the structures (Gilbert et al., 2006). Among the 63 stations investigated during the initial stock estimation, twelve stations were repetitively surveyed over the decade at Tatakoto (Fig. 1c). All these stations were located in the 0.5–2 m depth range of western lagoon.

The methods used in this study for sampling giant clam density were similar to those implemented in the previous surveys, to facilitate comparison between surveys (Gilbert et al., 2006). For Tubuai, the method consisted in the census and measurement to the nearest centimetre of all giant clams located in one-metre-wide belt-transects. The length of belt transects were function of the space available, ranging from 5 m for small patch reefs to 20 m on reef flats and ridges. For Tatakoto, where densities observed in 2004 could reach several hundred of individuals per square metre (Gilbert et al., 2005), two to three quadrats were disposed on giant clam aggregates along Line Intersect Transects (LIT). All giant clams found inside the quadrats were measured to the nearest centimetre. In this case, giant clam density was calculated as the product of their number inside quadrats and the percentage cover of live giant clams observed along the LIT (Gilbert et al., 2006).

Except for a small number of permanent transects performed at Tubuai ($n = 14$), transects were not permanently established. But the location of stations were geo-referenced (handheld GPS Garmin), and transects were always performed at similar depth and on the same habitat with a 10–50 m uncertainty. In most cases, belt-transects covered most of the space available (e.g., in lagoon patch reefs, ridges), therefore decreasing the variability of measurement locations. However, measured giant clams were therefore unlikely the same between surveys.

2.3. Model structure

The lagoon of Tatakoto and Tubuai were subdivided in a mosaic of data-driven management planning unit (DDPU, *sensu* Van Wynsberge et al., 2015). Maps of giant clam density, susceptibility to mass mortality and fishing pressure established by Van Wynsberge et al. (2015) for Tatakoto and by Van Wynsberge (2016) for Tubuai were superimposed using the “Intersection tool of GIS Esri® ArcMap 10.1 software, in order to obtain one single map. This “map overlay” approach provided management planning units whom irregular shapes are directly driven by the distribution of each spatial data layer (Van Wynsberge et al., 2015).

The population dynamics model previously established by Van Wynsberge et al. (2013) was improved on the basis of the new datasets and knowledge acquired, and was implemented for Tatakoto and Tubuai. For each DDPU, the model projected stocks over time (100 simulations) using size-based transition matrices (Caswell, 2001). Size distribution at time $t + 1$ (N_{t+1}) were iteratively calculated from size distribution at time t (N_t), using Eq. (1):

$$N_{t+1} = AN_t + \hat{R} - Q_f - Q_a \quad (1)$$

where A is a matrix which integrated growth and natural mortality, \hat{R} is recruitment, and Q_f and Q_a the numbers of fished wild individuals per size class for the meat and aquarium market

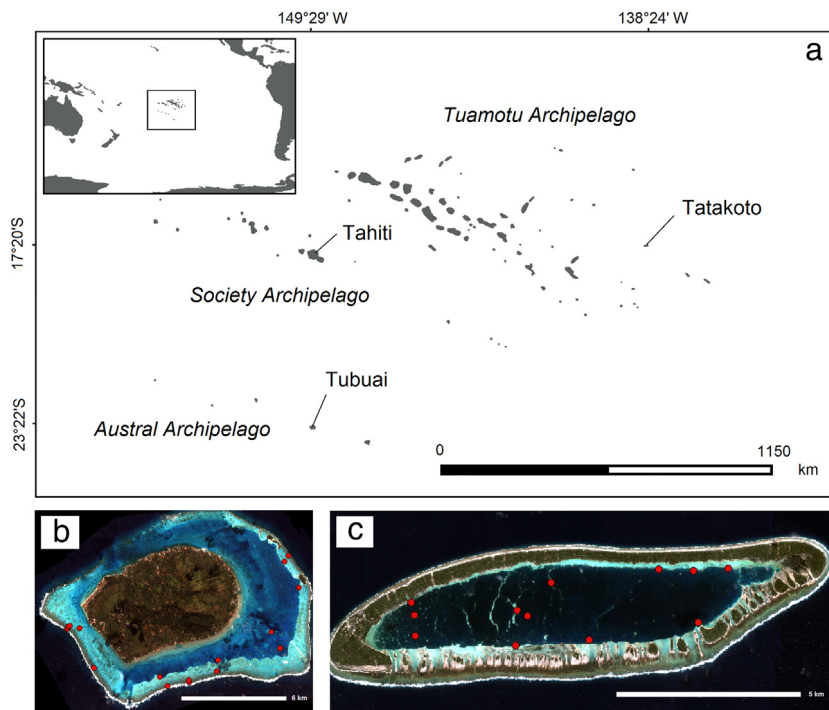


Fig. 1. Location of studied sites. (a) Map of French Polynesia highlighting the location of Tatakoto in the Tuamotu Archipelago and Tubuai in the Austral Archipelago. (b–c) Satellite images and monitoring stations (red dots) at Tubuai and Tatakoto. Only stations surveyed during each field campaign are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

respectively. Since growth rate was dependent on the season (Van Wynsberge et al., 2017), the selected time step was six months, with alternatively a warm and a cool season. All calculations were performed using software R3.1.0.

2.4. Model parameterization

- **Initial stock and size structure** N_0 : The surveys performed in April 2004 at Tatakoto and in December 2004 at Tubuai were considered as starting points for the population models (t_0). Giant clam densities were averaged per habitat on the basis of the habitat typology specifically designed to capture *T. maxima* densities at Tatakoto and Tubuai by Gilbert et al. (2006). For each planning unit designed by Van Wynsberge et al. (2015), the densities (\pm SD) per size class estimated on field were used to generate starting densities considered in the simulation, which were multiplied by habitat area (m^2) within the planning unit to provide an estimation of stocks (N_0).

- **Parameterization of matrix A** : Each term a_{ij} of the matrix A is the probability that a giant clam of size class i at time step t reaches the size class j at time $t + 1$. For a specimen of size class i , a_{ij} is the product of the probability of survival and probability of growth until size j between t and $t + 1$. Values for growth came from Van Wynsberge et al. (2017). Van Wynsberge et al. (2017) also estimated the instantaneous rate of natural mortality (M) at the two study sites. They found higher values for M at Tatakoto than at Tubuai. The instantaneous rates of natural mortality decreased with shell length at Tatakoto, but was relatively constant across all shell lengths for Tubuai (see Fig. 6 in Van Wynsberge et al., 2017). At intra-lagoon scale for Tatakoto, M was lower in the south part of the lagoon (recorded M values were $5.9 \times 10^{-4} \text{ day}^{-1}$ and $M = 8.5 \times 10^{-4} \text{ day}^{-1}$) than for other areas ($M > 1.9 \times 10^{-3} \text{ day}^{-1}$). No significant differences of M were found between tagging stations at Tubuai, and for both lagoons, M was not affected by any seasonal trend. In this study, survival per time step ($S_{\Delta t}$) was deduced

from these instantaneous rates of mortality (M) estimated by Van Wynsberge et al. (2017), using Eq. (2).

$$S = e^{-M(\Delta t)}. \quad (2)$$

- **Parameterization of recruitment \hat{R}** : We modelled recruitment inside each spatial planning unit as a Poisson distribution. The parameter of the distribution was a function of lagoon stock ($N_{\text{lagoon},t}$) and the proportion of recruits of the lagoon which fall inside each spatial planning unit (R_{pu}), following Eq. (3).

$$\hat{R} \sim P(f \times F \times N_{\text{lagoon},t} \times R_{pu}) \quad (3)$$

F is the relative contribution of the various size classes to reproduction: their values were established on the basis of gonad weight. Since giant clams are protandrous hermaphrodites, the gonad weight was split according to the relative proportion of female versus male part in the gonad issued from Menoud et al. (2016) for the two study sites. Spawn frequency and intensity, fecundity (i.e., percentage of fertilized eggs), and survival of eggs and larvae and juveniles between t and $t + 1$ were unknown, and were therefore grouped under a fertility rate f (sensu Caswell, 2001). A wide range of values were systematically tested for f (from 0.1 to 10^3 , in step of 0.001). The product $f \times F$ represented the number of recruits (0 cm) produced per individual per size class. When multiplied by $N_{\text{lagoon},t}$, it represented the number of recruits produced at lagoon scale, for which only a proportion R_{pu} fall inside the considered spatial planning unit. R_{pu} was considered constant over time and established on the basis of the number of 2–4 cm sized-clams observed in the field. We only considered the 2–4 cm size to estimate R_{pu} since very small individuals (<2 cm) could easily be missed during the censuses.

- **Parameterization of fishing pressure for meat Q_f** : Quantities of meat (kg) fished at lagoon scale were established using data collected in 2011 at Tubuai (local consumption and expeditions towards Tahiti) by the local fishery service (Direction des Ressources Marines et Minières, DRMM), and the monitoring of expeditions

performed monthly from 2006 to 2009 and from 2011 to 2014 at Tatakoto. Local consumption at Tatakoto was considered constant over time and was fixed at 2731 kg an^{-1} on the basis of interviews conducted with local inhabitants (Van Wynsberge et al., 2015). Since no reliable data were available in 2004, 2005 and 2010 at Tatakoto, the amount of meat fished during these years were considered identical to the nearby corresponding years (respectively 2006 and 2009). At Tubuai, where estimations were available for 2011 only, the amount of meat fished was considered constant over the study period.

The amount of meat harvested at lagoon scale was translated in number of individuals per size class and per spatial planning unit (Q_f) using (i) the mean catch of meat per fishers (ii) the relative proportion of fishers in the overall population, (iii) the maps of fishing grounds, (iv) the giant clam size classes targeted by fishers, and (v) the biometric relationships between the commercial weight and shell length. All data used for Q_f calculation came from Van Wynsberge et al. (2015).

- **Parameterization of fishing pressure for living specimen** Q_a (aquarium trade): The estimates of catches of wild living specimen at Tatakoto were available for this study period (unpublished data from DRMM). In order to decompose these catches at lagoon scale into catches for each spatial planning unit, we considered the same fishing grounds as those established for meat fishing pressure.

2.5. Scenarios of population dynamics for the 2004–2014 period

Considering the uncertainty on the parameters for natural mortality as well as its variability along the past decade, especially at Tatakoto, the model was first used to test the hypothesis that the giant clam population has been affected by an abrupt mortality event during the past decade. Specifically, we used the model to test several scenarios with different values and curve shapes of natural mortality rates. A first scenario (thereafter named “SM-1”) considered the values of natural mortality rates as estimated *in situ* by Van Wynsberge et al. (2017) on the 2012–2014 period. A second scenario (“SM-2”) considered that mortality rates by the Van Wynsberge et al. (2017)’s sampling protocol were overestimated, and allowed for higher survival rates across the 2004–2014 period. Finally, two last scenarios (“SM-3” and “SM-4”) considered respectively a progressive *versus* sudden increase of mortality rates during the decade. In these cases, survival rates were multiplied by a factor dS which decreased along time following a antilogistic curve (see Fig. S1 in Supplementary Materials).

Modelled stocks and size structures were assessed by comparison of simulated densities (d_s) and observed densities (d_o) for each survey time and each size class through the calculation of a R^2 term (4):

$$R^2 = 1 - \frac{\sum (d_o - d_s)^2}{\sum (d_o - \bar{d}_o)^2}. \quad (4)$$

2.6. Scenarios of long term population dynamics

In this section, we describe how the model was used to identify which management strategies are the most efficient to sustain giant clam stocks considering the past and current environmental conditions, and evaluate the extent by which these strategies remain efficient if mortalities increase during the next century.

The model projected stocks over a period long enough (100-years, i.e. 200 time steps) to integrate several generations of giant clams, and compare the long term dynamics of stocks between Tatakoto and Tubuai according to various management scenarios and regimes of natural mortality triggered by climate variability.

For natural mortality, the survival rates (S) estimated *in situ* by Van Wynsberge et al. (2017) were weighted by a factor dS

which followed a Gaussian distribution of mean dS_m and standard deviation dS_{sd} . We introduced temporal autocorrelation using the Markov chain described in Eq. (5):

$$dS_t \sim \frac{a(dS_{t-1}) + \aleph(dS_m, dS_{sd})}{a + 1} \quad (5)$$

where a controls for the strength of the temporal autocorrelation. Increasing dS_m induced a higher mean survival rate over the study period, while increasing the factor a increased the temporal autocorrelation. As a specific case, fixing a to 0 induced survival rates that were independent one time step to another (See Fig. S2 in Supplementary Materials), while fixing $a > 0$ induced non regular inter-annual cycles in mortality rates as expected for resources affected by ENSO. We tested a wide range of values for dS_m and dS_{sd} and a , and for each couple of values we analysed the resulting dynamics of projected stocks.

For management planning, we tested (1) various levels of reduction of fishing effort (i.e., 0%, 20%, 40%, 60%, 80% and 100% reductions of Q_f); (2) an increase in the minimum allowable size for catch (i.e., from 12 cm to 13 cm, 14 cm, 15 cm, 16 cm and 17 cm); and (3) closing to fishing various proportions of the area for which Van Wynsberge et al. (2017) evidenced the lowest natural mortality of giant clams. We tested No-Take-Areas of 0, 5000, 10 000 and 20 000 m^2 . The tested restrictions were only applied on fishing for meat (Q_f) and did not affect fishing for the aquarium trade (Q_a).

The long term dynamics of stocks among the various scenarios was compared on the basis of the Area Under Curve (AUC) of projected biomass rather than using the population growth rate, the latter being poorly informative when stocks are highly variable. Area Under Curves were calculated using the `lintegrte` function of package `tis` in R.3.1.0.

2.7. Statistical analyses

Giant clam densities were log transformed, and differences between monitoring sessions were tested using a linear model (function `summary.lm` in R.3.1.0.). The normality and homogeneity of variances of residuals were checked using quantile–quantile plots and scale location plots of `sqrt(|residuals|)`. Statistical analyses were performed on the basis of stations common to the various monitoring sessions only ($n = 12$ for Tatakoto and $n = 16$ for Tubuai).

3. Results

3.1. Monitoring of *T. maxima*'s densities

In this section, we describe the results of the *in situ* temporal monitoring of giant clam densities and size frequency distributions. These results were used to validate the population models (see Section 3.2).

Stock estimates decreased significantly over the decade at Tatakoto, then stabilized in 2013 (Fig. 2a). Size frequency distributions at lagoon scale were contrasted between surveys, with a large proportion of small giant clams in 2004 (mode = 4 cm, Fig. 2c, vs mode = 11 cm in 2014, Fig. 2g).

At Tubuai, estimated abundances of giant clams were stable over the decade (from $5.8 \times 10^6 \pm 0.9 \times 10^6$ in 2004 to $4.9 \times 10^6 \pm 0.9 \times 10^6$ in 2014, Fig. 2b) with no significant differences between surveys ($F = 0.27$, p -value = 0.85). Size structures at Tubuai were systematically skewed towards large specimens for all surveys (mode ranging from 14 to 15 cm, Fig. 2d,f,h).

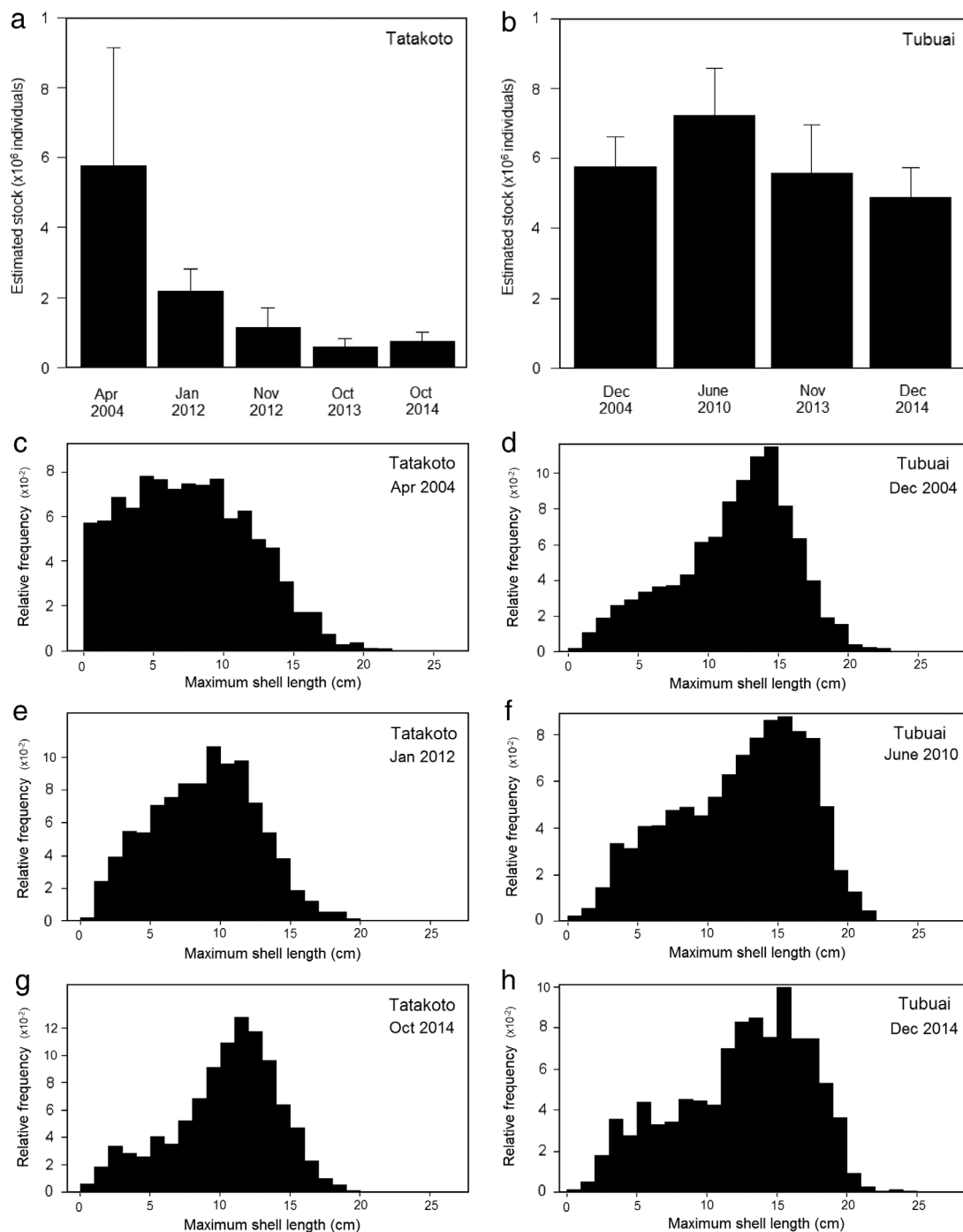


Fig. 2. Estimated abundances and size structures of *Tridacna maxima* at the two studied sites. (a–b) Abundances. Error bars are 95% confidence intervals; (c–h) size structures. Left panels: Tatakoto, right panels: Tubuai. Note that the stock presented here is relative to habitats covered by the sampling stations common to all field trips; this stock is used here for model validation purpose, but do not represent the actual stock of the lagoons computed with all available stations.

3.2. Scenarios of population dynamics for the 2004–2014 period

The objective of this section was to address if theoretical population dynamics support the hypothesis that giant clam populations have been affected during the past decade by a mass mortality that occurred punctually and suddenly, as expected if triggered by climate variability.

For Tatakoto, poor congruence between the observed and the simulated abundances and size structures was found ($R^2 = 0.12$) when natural mortality was set to the values estimated by Van Wynsberge et al. (2017), suggesting that natural mortality

estimated from field tagging during the 2012–2014 period poorly reflected natural mortality of giant clams during the past decade. Considering lower natural mortality rates than those estimated by Van Wynsberge et al. (2017) significantly increased the congruence between the observed and the simulated abundances and size structures ($R^2 = 0.38$), but the best congruencies were obtained when considering natural mortality variable over the decade (Fig. 3a and b). In this latter case, considering a sharp increase of natural mortality rates performed better than considering a progressive increase of natural mortality rates ($R^2 = 0.55$ and 0.44 respectively).

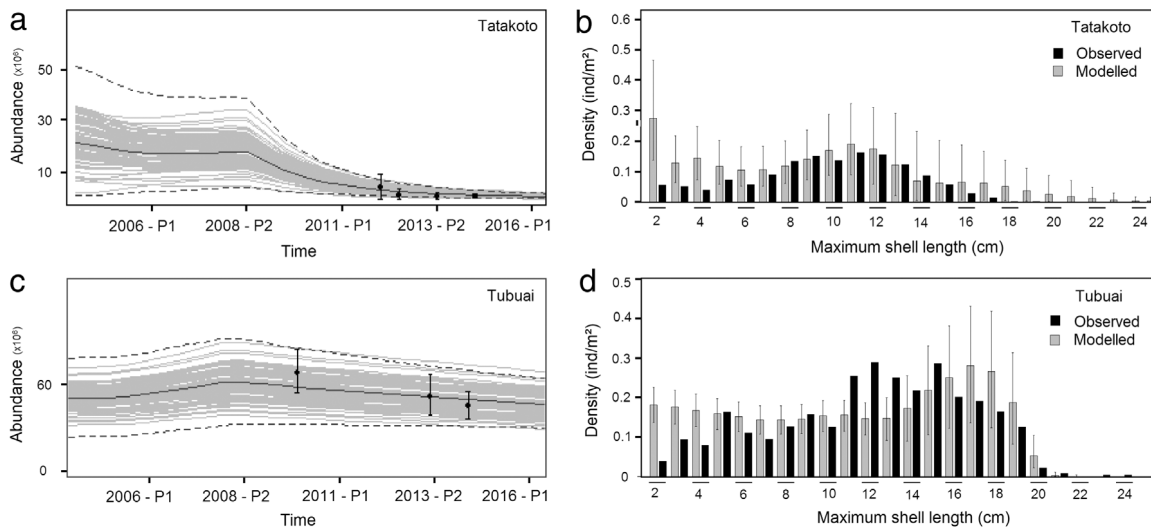


Fig. 3. Projected short term dynamics that provide best agreement with the observed stocks. Panels (a) and (c) display population projections (100 simulation, grey curves) and their median (solid black line), 0.05 and 0.95 quantiles (dashed black lines). Black points and error bars are abundances and 95% confidence intervals estimated from the field. P1 and P2 refer to the warm and cool periods of the year respectively. Panels (b) and (d) display the size frequency distributions observed from field work in October 2014 for Tatakoto and in December 2014 for Tubuai (black), and the modelled size frequency distributions (median) for the corresponding periods (grey). Error bars are 0.05 and 0.95 quantiles.

Table 1

Adequacy between simulated and observed stocks for the short-term scenarios. The term f refers to fertility, dy to mortality and $antilog$ to the shape of antilogistic curves for mortality (see Fig. S1 in Supplementary Materials). SSres is the sum of squared residuals.

Island	Scenarios	f	dy	Antilog	SSres	R_2
Tatakoto	SM-1	157.00	1.16	A	1.890	0.120
	SM-2	27.70			1.330	0.380
	SM-3	32.00			1.210	0.438
	SM-4	37.00			0.959	0.553
Tubuai	SM-1	3.97	1.03	A	0.626	0.708
	SM-2	2.44			0.449	0.791
	SM-3	2.39			0.409	0.810
	SM-4	2.38			0.399	0.814

For Tubuai, the congruence between the observed and the simulated abundances and size structures was systematically higher than for Tatakoto, with R -square values ranging from 0.71 to 0.81. Similarly to Tatakoto, the model better reproduced the observed stocks of Tubuai when considering natural mortality variable over the decade (Fig. 3c, d). In this case however, considering either a sharp or progressive decrease of natural mortality provided similar results ($R^2 = 0.814$ and $R^2 = 0.810$ respectively).

For all scenarios of natural mortality tested, only fertility rates an order of magnitude higher at Tatakoto than at Tubuai could adequately reproduce the observed abundances and size frequency distributions (f ranging from 37.0 to 157 at Tatakoto and from 2.38 to 3.97 at Tubuai, Table 1).

3.3. Scenarios of long term population dynamics

The objective of this section was to identify which management strategies are the most efficient to sustain giant clam stocks considering the past and current environmental conditions, and evaluate the extent by which these strategies remain efficient if mortalities increase during the next century.

When stocks were projected over 100 years under various mortality regimes, increasing the mean survival (dS_m) while maintaining other parameters constant systematically increased AUC (See Fig. S3 in Supplementary Materials). When dS_m was fixed to 1.1 for Tatakoto and to 1.02 for Tubuai, biomass at the start of the simulation fell in the confidence interval of biomass (5% and 95%

quantile on 100 runs) at the end of the simulations (Fig. 4c and d). In this case, increasing the variability of survivorship dS_{sd} from 0.01 to 0.05 and 0.1 decreased stocks towards extinction when the autocorrelation parameter was fixed to low values (Fig. 4e and f). By contrast, increasing both dS_{sd} and the strength of autocorrelation (a) increased the variability of stocks (Fig. 4g and h). For all scenarios, stock variability was systematically higher for Tatakoto than for Tubuai.

The impact of management on simulated stocks was relatively low (systematically $\leq 62\%$ increase of AUC) for all scenarios of natural mortality (Fig. 5). When variability of natural mortality was low ($sd = 0.01$) and no autocorrelation was considered ($a = 0$), the best management strategy was a decrease of fishing pressure. For example, decreasing fishing pressure from 100% to 40% induced a 62% increase of AUC at Tatakoto. By contrast, increasing the minimum legal size and closing areas to fishing were less efficient: AUC increased by 23% when legal size increased from 12 cm to 15 cm and AUC increased by 0% when area closed increase from 0 m² to 20,000 m² at Tatakoto (Fig. 5e). This pattern remained valid for Tubuai and when variability of mortality was high ($sd=0.1$) though in this case differences in AUC were blurred by larger variability (see error bars representing 0.05 and 0.95 quantiles in Fig. 5).

4. Discussion

4.1. Strength and limitation of the population model

The population model used in this study was established following that introduced by Van Wynsberge et al. (2013). Similar to the initial version, our new model was constrained primarily by habitat distribution and giant clam densities per habitat type; hence it remained a true spatial model. Our new model also refines considerably relevance and knowledge available for managers. Indeed, stocks are fished at a very local scale, and management action and their impacts can be analysed at the same level, increasing the relevance of a management plan for local stakeholders (Van Wynsberge et al., 2013). In this study, we used a data driven approach to design spatial planning units; this approach was useful to integrate data on life traits (e.g., survival rate, growth rate) and fishing pressure (e.g. fishing grounds and yields), and to save the

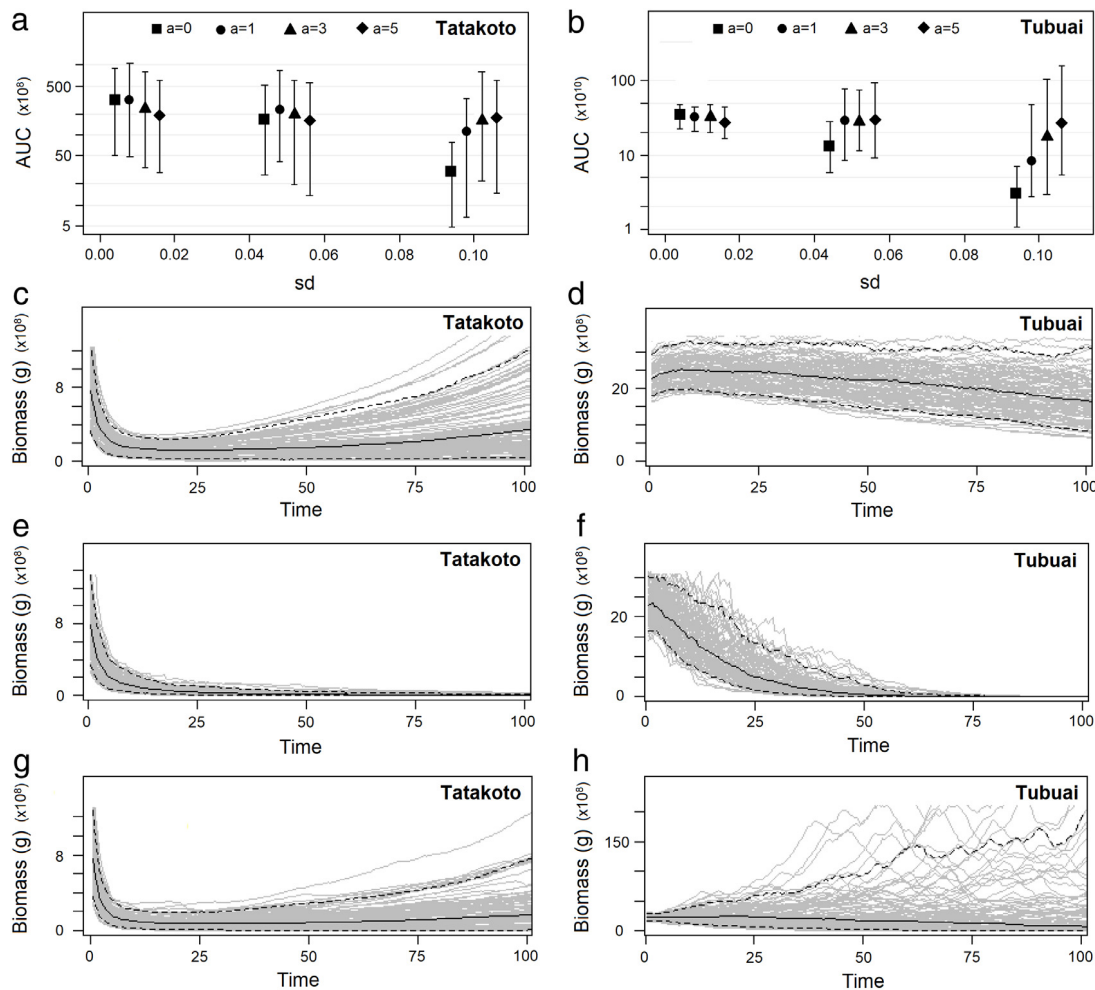


Fig. 4. Projected long term dynamics of biomass and area under biomass curve for various levels of variability for survival rates (Ssd) and autocorrelations (a). (a) Area under biomass curve (AUC) for Tatakoto. (b) Area under biomass curve (AUC) for Tubuai. (c) $Sm = 1.1$ $Ssd = 0.01$ $a = 0$ for Tatakoto (d) $Sm = 1.02$ $Ssd = 0.01$ $a = 0$ for Tubuai (e) $Sm = 1.1$ $Ssd = 0.1$ $a = 0$ for Tatakoto (f) $Sm = 1.02$ $Ssd = 0.1$ $a = 0$ for Tubuai. (g) $Sm = 1.1$ $Ssd = 0.1$ $a = 5$ for Tatakoto. (h) $Sm = 1.02$ $Ssd = 0.1$ $a = 5$ for Tubuai. Error bars in panels (a) and (b) are 0.05 and 0.95 quantiles.

initial resolution of data to avoid approximation by aggregation to arbitrary regular squares or hexagons as it is commonly performed elsewhere (Van Wynsberge et al., 2015).

Moreover, a number of improvements from Van Wynsberge et al. (2013)'s initial version were implemented. First, we used size classes rather than age classes for model structure. Age is hard to determine in the field without complex, expensive and destructive methods (e.g., sclerochronology); it is often determined from indirect methods (e.g. growth curves). By contrast, size is directly measurable in the field, and is the measure of reference for size based management strategies (i.e. minimum legal size limit). Second, fishing mortality was deduced from total mortality in Van Wynsberge et al. (2013)'s model, but was directly integrated as the number of fished giant clam in this study. We believe the latter option more adapted to small Pacific islands in the context of climate change, because the overall mortality can be highly variable depending on climate conditions (especially for atoll lagoons), while fishing effort is primarily induced by frequent orders from Tahiti's market and therefore remain fairly constant over time. Third, in this study we integrated stochasticity in the model parameters. As such, the enhanced model is a useful and powerful tool to analyse population dynamics of lagoon resources affected by highly fluctuating environment. Finally, the efforts implemented in field surveys to estimate model's parameters were an order of magnitude higher compared to the previous model. They were

also estimated for a semi-closed atoll lagoon, a context which was missing in Van Wynsberge et al. (2013).

Nevertheless, some limitations of the population model are worth to be pointed out. In this study, we did not consider inter-island connectivity in the model. Genetic studies suggest a relationship between genetic connectivity and geographical distance at the scale of an Archipelago (Laurent et al., 2002), but do not address the scale of demographic connectivity. The rate of larval export through reef passes has been estimated at 1% of the overall larval stock for pearl oysters in the open atoll, French Polynesia (Thomas et al., 2012), and is likely an order of magnitude lower for semi-closed atoll without reef passes. Considering the distance between atolls in the eastern Tuamotu Archipelago and lagoon enclosure of atolls in this area, the number of recruits coming from other islands to Tatakoto must be negligible compared with local recruits. This may be less true for the open lagoon of Tubuai, and more extensive studies on the current larval connectivity would help refining the population model. Beyond the current larval connectivity, theoretical studies suggest that climate change may affect connectivity of tropical species (Kleypas et al., 2016), but this remains unquantified for French Polynesia's giant clams.

Finally, while the variance of observed density is well explained by the model for Tubuai (up to 81% of variance explained), the model is less satisfying for Tatakoto (55%). This suggests that additional processes occur, that are not adequately captured by

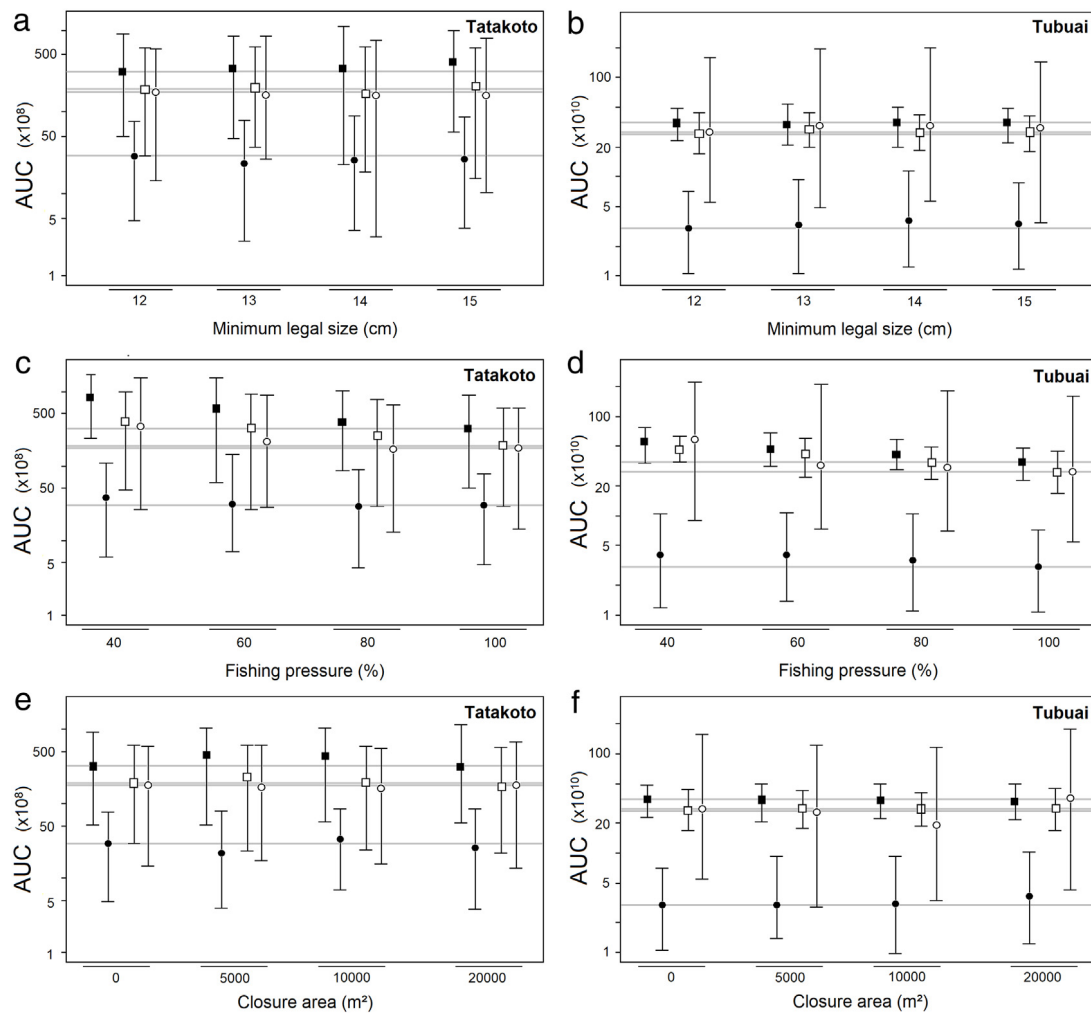


Fig. 5. Projected long term dynamics of area under biomass curve for various management strategies, variability for survival rates (Ssd) and autocorrelations (a). Square: Ssd = 0.01 Circle: Ssd = 0.1 Black: $a = 0$; White: $a = 5$. Error bars are 0.05 and 0.95 quantiles.

the model. Despite our attempt to sample data for a subset of stations for all habitats, model parameters could be monitored *in situ* for a short period only (2012–2014) and for a limited number of stations. Giant clam life history traits (e.g., growth, mortality, recruitment) appear highly variable both spatially and temporally, which suggest that correct estimations of these parameters require extensive and intensive monitoring (Yau et al., 2014). Generalization across the spatial domains require caution and we recommend to conduct spatially explicit surveys as well for all future studied lagoons for a better model parameterization. Van Wynsberge et al. (2013) recommended a twice-yearly monitoring for these parameters; we here further recommend that the monitoring need to be performed during a sufficiently long period to capture the inter-annual variability of these parameters.

4.2. Giant clam population dynamics in open versus closed lagoons

The projections of stocks and their validation by *in situ* data along the 2004–2014 period highlight that only a fertility f an order of magnitude higher at Tatakoto than at Tubuai can explain the observed stocks and size structure. A clear understanding of the processes leading to high fertility at Tatakoto is beyond the scope of this study, but we expose hereafter how reef type and lagoon enclosure may be involved (Van Wynsberge et al., 2016).

The degree of lagoon enclosure may promote population isolation and increase self-recruitment rate, if water time residence is

high (Sponaugle et al., 2002). In closed and semi-closed lagoons, water residence time is estimated to range from 10 to 100 days (Andréfouët et al., 2001), which is an order of magnitude higher than the pelagic life duration of giant clam's larvae (10–14 days, Jameson, 1976). Since recruitment success is partly determined by the ability for larvae to find a hard substrate (Dumas et al., 2014), the water time residence in atoll lagoons increase the probability for larvae to fix on suitable habitats. By contrast, in the open and isolated lagoon of Tubuai, the low residence time of lagoon water prevent many larvae to find a suitable substrate in the lagoon before being evacuated towards the ocean where the probability to find a favourable substrate is low in general (Pineda et al., 2009), and most likely null after leaving a remote island like Tubuai. High mortality therefore affects larvae in open lagoons and decrease fertility *sensu* Caswell (2001).

High self-recruitment rates promote geometric growth of giant clam populations (Yau et al., 2014). Therefore, a closed lagoon forces the giant clam dynamics towards exponential growth when fertility and/or survivorship are high, or towards exponential decrease of abundances when fertility is low, or when mortality of adult specimens is high. Giant clam populations that are characterized by high self-recruitment rates are also more apt to exponential growth when environmental conditions are locally propitious to survival. Larvae produced by closed populations directly benefits local recruitment, which itself increases local brooding stock, and the cycle can potentially continue. This process may lead to a fast

increase of abundances if favourable conditions persist locally. The huge 2004 stock we observed in Tatakoto are likely the results of such dynamics.

Beyond self-recruitment rate, density dependent processes may also increase fertility. First, the synchrony of spawns via pheromones increases the probability for gametes to meet and therefore increase reproductive success (Teitelbaum and Friedman, 2008; Braley, 1984). Second, larvae tend to fix preferentially on adult shells via chemical cues (Dumas et al., 2014), and high density of adult shells provide extensive suitable substrate for juveniles. Positive density-dependent processes therefore increase fertility in area of high densities. Thus, in closed or semi-closed lagoons, high self-recruitment rates tend to increase both reproductive success and density, promoting very high stocks as far as environmental conditions remain propitious for survival, sometimes during decades. This process may explain that densities of several tens to hundreds of individuals per square metres have been observed in several atoll lagoons of Tuamotu archipelago (Gilbert et al., 2005, 2006), but never in open lagoons.

4.3. Climate variability and mass mortalities in enclosed atoll lagoons

A mass decrease of giant clam abundances occurred in Tatakoto in 2009 (Andréfouët et al., 2013). Similar loss was also evidenced in Fangatau (Andréfouët et al., 2015). In 2016, a decrease of abundance was also evidenced at Tatakoto and Reao (unpublished data) following this time a mass bleaching event triggered by a particularly warm El Niño. While these 2016 mass mortalities were undoubtedly related to high temperature, the exact causes of previous mortality events remain unknown, although changes in water lagoon conditions were likely part of the process. An unusually long period of low wind, low swell combined with high temperature could isolate the lagoon from ocean, and modify the physical properties of the lagoon water (Andréfouët et al., 2013, 2015). Other hypotheses were considered to explain the 2009 mass mortality at Tatakoto: proliferation of predators, parasites, pathogens, or autoregulation due to high densities via negative density dependence processes (Van Wynsberge et al., 2017). Here, we show that the simulated stocks and size structures were more congruent with observations when mortality was increased suddenly during the past decade, as it could happen after an acute mortality event (Fig. 3, Table 1). Our results need to be considered with caution, as the population model only partially explained stock variability for Tatakoto (55% of variance explained). A sudden change in mortality is coherent with an episode of abnormal climate conditions affecting Tatakoto's lagoon. The model, however, also suggests that mortality rates remained high from 2009 to 2014. This is also supported by monitoring of natural mortality performed between 2012 and 2014 (Van Wynsberge et al., 2017). Further research need to determine why mortality rates remained high during such a long period.

In this study, we highlighted that an increase of variability in mortality rate decreased stocks, unless temporal autocorrelation of mortality rates was high (Fig. 4). In the case of high autocorrelation, stocks could either reach high or low values, depending on the duration and intensity of favourable/unfavourable periods for survival. These results mean that, even for a long life and slowly growing species like *T. maxima*, stocks can be highly variable if mortality rates fluctuate according to inter-annual changes in environment (e.g. ENSO). Stocks reached greater values for Tubuai than for Tatakoto during periods propitious to survival in our simulations, due to a greater initial population size at Tubuai. Considering the tenfold decrease of stocks at Tatakoto during the last decade, there is little likelihood that stocks will return to the 2004 values before several decades, unless fertility and survival reach enormous values during a long period.

4.4. Managing giant clams facing mortality events: which strategy for islands and atolls in French Polynesia?

The high variability of natural mortality rates evidenced during the past decade combined with a long term scenario meant that the influence of management on stocks was limited. Among the various management strategies tested, the most effective was a reduction of fishing effort (62% increase of AUC for Tatakoto when fishing effort was reduced at 40%). A reduction of fishing effort was found more effective than other measures because no take areas and size limits, by contrast, only transfer fishing pressure on other areas or size classes. These results remained relevant for the two study sites and for all mortality regimes tested, and are in line with previous models on giant clam species in French Polynesia (Van Wynsberge et al., 2013). Reducing fishing pressure through the implementation of quotas could be relevant for isolated islands and atolls and easily monitoring in practice, since all catches for commercial exploitation follow the same transit route (i.e. cargos and planes).

While quotas appear to be the most efficient tools to ensure sustainable fisheries in French Polynesia, they are unfortunately the less acceptable by the population. Traditionally, Polynesian islanders used to implement rotational and non-permanent closures (locally called “Rahui”) and NTAs (“Tapu”, or “Tabu”) to manage their own resources. As such, NTAs (and rotative closures) are generally well understood and accepted by inhabitants. Official NTAs have already been implemented specifically for giant clams by the DRMM at Tatakoto and Reao atolls. Unfortunately, our results suggest that NTAs are the less efficient way to manage the current exploitation for commercial purpose.

The efficiency of minimum legal sizes appears to be of intermediate efficiency between quotas and NTAs. The 12 cm minimum legal size for giant clams, while not as traditional as NTAs, has been applied to the entire French Polynesia since 1988, and is now well rooted in the inhabitant's practices. Through less efficient than quotas, increasing the minimum legal size may be a good alternative that could meet good level of compliance (Yau, 2011).

4.5. Resource management facing climate change

The sea temperature is expected to increase by at least 1 or 2 °C during the next century (Gattuso et al., 2015), in the least dramatic scenario. Unusual periods of low wind, low waves and high temperature that increase the risk of mass mortality in Pacific atoll lagoons are also expected to increase in the future (Andréfouët et al., 2015). Thus, events of high mortality triggered by climate variability and anomalies are expected in the near future in Pacific atolls and islands. While management of lagoon resources have focused on fishing pressure during the past decades, it is now evident that management also needs to account for climate variability (Bell et al., 2011). Our study highlights that, in the face of climate change, the efficiency of current management measures is expected to decrease.

This study contributes to the application of theoretical population biology to real-case management studies, for islands likely to meet significant environmental issues in the near future due to climate change and unusual climatic conditions seldom met in the past but more frequent in the future. While in some ways, the study was data-limited, it was also data rich with temporal surveys providing realistic constraints on the input and output of the scenarios; As such it is representative of many reef fishery contexts where some data exists, but many gaps as well. Overall, the study is constrained much better than what could be possible to achieve for many other island fisheries. Yet, with this study, managers have access to a theoretical and practical framework to study population dynamics in the future, pending they can parameterize adequately

the necessary input variables. The ability of insular populations and managers to integrate climate effects on resource dynamics across several decades and plan for the required changes will determine their ability to cope with climate change and maintain ecosystem services, food security, incomes and a resident island population.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.tpb.2017.10.005>.

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